

Dispersal without errors: symmetrical ears tune into the right frequency for survival

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Vertebrate animals localize sounds by comparing differences in the acoustic signal between the two ears and, accordingly, ear structures such as the otoliths of fishes are expected to develop symmetrically. Sound recently emerged as a leading candidate cue for reef fish larvae navigating from open waters back to the reef. Clearly, the integrity of the auditory organ has a direct bearing on what and how fish larvae hear. Yet, the link between otolith symmetry and effective navigation has never been investigated in fishes. We tested whether otolith asymmetry influenced the ability of returning larvae to detect and successfully recruit to favourable reef habitats. Our results suggest that larvae with asymmetrical otoliths not only encountered greater difficulties in detecting suitable settlement habitats, but may also suffer significantly higher rates of mortality. Further, we found that otolith asymmetries arising early in the embryonic stage were not corrected by any compensational growth mechanism during the larval stage. Because these errors persist and phenotypic selection penalizes asymmetrical individuals, asymmetry is likely to play an important role in shaping wild fish populations.

Keywords: fluctuating asymmetry; sound; dispersal; recruitment; population dynamics; otoliths

1. INTRODUCTION

Dispersal is one of the key mechanisms shaping the geographical distribution and persistence of species in both terrestrial and marine systems (Clobert *et al.* 2001). During dispersal, individuals are faced with the major challenge of constantly gathering information on the variable conditions of the surrounding environment in order to survive (Dall *et al.* 2005; Cote & Clobert 2007). In coral reef fishes, the question of how centimetre-sized larvae orient themselves towards coral reefs following weeks of dispersal at sea remains one of the biggest unsolved questions in marine science. However, the smell and sound of coral reefs have recently been demonstrated to be significant navigation cues for the successful recruitment of reef fishes to benthic habitats (Simpson *et al.* 2005a; Gerlach *et al.* 2007).

Reef sound, in particular, has emerged as a leading candidate mechanism, because acoustic signals can propagate in water over many kilometres and with little attenuation (Rogers & Cox 1988). Although experimental evidence of the hearing abilities of reef fish larvae is only recent and limited, we now know that pelagic reef fish larvae home in on reef-associated sounds to actively locate and move towards their juvenile and adult benthic reef habitats (Leis *et al.* 2003; Simpson *et al.* 2004; Tolimieri *et al.* 2004; Wright *et al.* 2005). Yet given that coral reefs are particularly noisy environments (Cato 1978), the detection and selection of the appropriate settlement habitats may be

easily obscured by a suite of sound sources of mixed frequencies and intensities. In reef environments, low-frequency sounds are largely composed of background abiotic noises such as waves crashing, surface wind and current sheer; in contrast, the source of high-frequency sounds is mostly biological in origin such as the grunting and gurgling of nocturnal fishes and the crackling and snapping of crustaceans and other invertebrates (Simpson *et al.* 2004). By being capable of tuning into a specific frequency noise, pre-settlement larval fishes may get a better indication of the biological and physical states of the habitat they are approaching. Indeed, it has recently been demonstrated that settlement-stage larvae can actively discriminate between different components of reef sound, and some preferentially settle onto reefs that produce high-frequency noise above 570 Hz (Simpson *et al.* 2005a). To what extent the ability to detect sound at these high frequencies confers some selective advantage is unknown.

Clearly, the integrity of the sacculus, the primary auditory organ in fishes, has a direct bearing on what and how fish larvae hear. Sacculus otoliths are hard calcium carbonate stones and constitute an integral part of the hearing and equilibrium structure in fishes, and variations in the size and shape of otolith pairs may have a major bearing on an individual's ability to effectively detect sound (Popper & Lu 2000). Fishes depend on a comparison of left versus right sacculus input to the brain to resolve the azimuth of the sound direction (i.e. inter-sacculus analyses; Edds-Walton & Fay 2002), and morphological differences between the right and left paired sacculus otoliths can pose problems for sound localization due to incongruity in the movement of the right

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and left otolith within the saccule (cf. Lychakov & Rebane 2005). Hence, even a small degree of asymmetry in the shape of the otolith pair can cause significant differences in the acoustic functionality of young fishes, thereby potentially jeopardizing the successful recruitment of larvae to suitable benthic habitats.

Fishes provide a good model to explore functional costs of developmental asymmetries because they may be particularly susceptible to high levels of developmental error given that most morphological, physiological and behavioural changes occur rapidly and during a relatively short time period over the embryonic and larval stages of life (Fuiman & Higgs 1997). Consequently, developmental errors accumulating during these early life stages may have profound ramifications on individual and subsequent population fitness. Given these early life-history characteristics, the use of otolith morphology in studies of bilateral asymmetries seems particularly attractive for larval fishes because otoliths provide a reliable and permanent record of past growth events and are intrinsically shaped by, and sensitive to, both genetic and environmental conditions (Cardinale *et al.* 2004; Gagliano & McCormick 2004). Although the complexity of otolith shape can be regarded as an excellent morphological model to investigate functional aspects of developmental asymmetry, surprisingly few studies have used otoliths for this purpose (Somarakis *et al.* 1997; Gronkjaer & Sand 2003). So far, larval fish otoliths have been mostly used in this context to explore the causative factors responsible for the occurrence of asymmetries but not the functional costs to the individual.

How much of the variation in the ability of the larval fishes to locate sound accurately can be explained by variation in otolith morphology is at present unknown. Here, we investigate the ecological and evolutionary consequences of developing asymmetrical otoliths on individual and subsequent population fitness in a common coral reef fish (*Pomacentrus amboinensis* Bleeker 1868) at the settlement interface between the pelagic and demersal environment. Specifically, we examined whether otolith asymmetry compromises the ability of larvae to distinguish between different sound frequencies associated with optimal and suboptimal habitat as they approach the reef, and if so, what are the consequences for the successful replenishment of adult populations.

2. MATERIAL AND METHODS

(a) Study system

The study species was the Ambon damselfish (*P. amboinensis*), a common and abundant coral reef fish on the Great Barrier Reef. This species has a complex life cycle that begins in benthic nest sites where females lay eggs which are tended by a male until hatching (3–4 days). Following hatching, *P. amboinensis* larvae undergo a 15- to 23-day pelagic phase in the open ocean before returning to the reef, where they settle directly into adult coral reef habitats. Between the summer months of October to January, the numbers of larval recruits settling on the mid-shelf fringing reefs surrounding Lizard Island (Great Barrier Reef, Australia) are high and their timing predictable, making this species an excellent model for this study.

(b) Field sampling

Over 4 days in early December 2003, prior to dusk on the night of hatching, we collected a total of 12 clutches from a range of mid-shelf reef habitats around Lizard Island, so as to obtain a sample as representative as possible of the population reproductive output for that pulse. At hatching, samples of approximately 100 hatched individuals were collected from each clutch and preserved in 30% ethanol freshwater solution (Gagliano *et al.* 2006).

During the following new moon phase 15–20 days later that month, recruits from the same cohort (i.e. hatched during the same reproductive pulse) were captured as they approached the reef using six light traps. Four of these traps were equipped with underwater speakers, while a dummy barrel and speaker of equal dimensions was attached to the remaining two traps to control for any attraction of reef fishes to these floating objects. Traps were moored over sandy bottom approximately 500 m from the reef edge, 1 m below the surface and 180 m apart. This was established to be the optimal distance to ensure that the traps were close enough to be sampling from the same assemblage of larval fishes, while preventing sound interference and any light overlap between traps (Simpson *et al.* 2004). The sound system consisted of a 12 V marine battery powering a portable CD player through a 70 W amplifier through which high (more than 570 Hz) or low-frequency (less than 570 Hz) reef noises were broadcast at 156 dB relative to 1 μ Pa at 1 m. We used the same recording of the dusk chorus of biological noise recorded at a nearby mid-shelf reef habitat on the Great Barrier Reef during the new moon that had attracted settlement-stage coral reef fishes in previous studies (Simpson *et al.* 2004, 2005a). Briefly, it consisted of a 4 min looped section played throughout the night and made up of a chorus of pops made by nocturnal fishes together with a higher frequency (2.5–200+ kHz) but lower-intensity background crackle produced by snapping shrimps as well as other nocturnal feeding, movement and calling sounds. The high- and low-frequency filtered reef noises were obtained using bandpass filters, and the sound input was balanced so that equal sound energy (156 dB re 1 μ Pa at 1 m) was broadcast by each system. The dummy system produced no noise. The sound system was randomly relocated each night to avoid any confounding effects due to trap location. All traps were deployed just prior to dusk and cleared of fish just after dawn the following morning for a total of six consecutive nights.

(c) Data collection and analyses

To simplify the reporting and discussion of our findings, we use the term 'asymmetry' in a broad sense when referring to differences between the left and right sides of a trait that arise as a product of random developmental perturbations within an individual (i.e. fluctuating asymmetry (FA); Palmer & Strobeck 1986). To establish if otoliths exhibited FA, we calculated signed asymmetry values (R–L) for each individual fish. We then examined the distribution of these values in each otolith pair character to ensure that the characters used exhibited true FA (distribution with a mean equal to zero and normal variation), as opposed to different forms of asymmetry such as directional asymmetry and antisymmetry. We used a one-sample *t*-test to test for signs of directional asymmetry (skewed distribution) and a Shapiro–Wilks' statistic for antisymmetry (bimodality) as described by Palmer & Strobeck (1986). All characters under consideration had signed means not significantly different from zero

($p > 0.05$). When we tested kurtosis for each sample, all but five of the asymmetry distributions examined were leptokurtic (i.e. kurtosis values greater than zero). Because visual inspection of those asymmetry distributions that were not leptokurtic showed no evidence of directional or asymmetric distribution, we concluded that the asymmetry present was FA (Gangestad & Thornhill 1999). To eliminate the possibility of inflated asymmetry estimates due to measurement error (ME), after initial otolith measurements were completed all otolith characters on both right and left sides were randomly re-measured with no knowledge of sample identity. To test for the importance of non-directional asymmetry relative to ME, we used a mixed model ANOVA with otolith side as a fixed factor and individual as a random factor as described by Palmer & Strobeck (1986). The side effect tested for directional asymmetry, while the side \times individual interaction tested for non-directional asymmetry. None of the characters showed directional asymmetry (all $p > 0.05$). The interaction variance was highly significant for all characters under consideration ($p < 0.001$), indicating that ME variance was significantly smaller than FA variance, hence providing justification for FA significance tests among treatments (Palmer 1994). Since the direction of asymmetry was not of direct interest, we used absolute asymmetry to compare relative levels of FA between sound treatments.

To determine the frequency of FA in individuals at hatching, 30 newly hatched larvae were randomly subsampled out of 100 individuals collected at hatching from each clutch. The recently formed sagittal otoliths of individual hatchlings were located under a Leitz Dialux 22 compound microscope at $400\times$ magnification. The size (area, μm^2) of the left and right otolith was recorded as a measure of otolith size-at-hatching. This trait was independently re-measured for each hatchling without knowledge of previous measurements. Adopting an approach similar to Cornelissen & Stiling (2005), we then classified as 'asymmetrical' all individuals for which FA was greater than the ME for this trait. Here we assumed that hatchlings collected from benthic nests around Lizard Island were a representative sample of the otolith size-at-hatching of *P. amboinensis* of that same cohort that survived the pelagic phase to return and settle on the fringing reefs around the island. While this is an untestable assumption, we believe that it is acceptable given recent evidence indicating a high degree of self-recruitment at this location for this species (Jones *et al.* 1999; James *et al.* 2002).

After the variation in the degree of asymmetry among replicate nights of collection and light-trap pairs used within treatments was examined for all 19 otolith shape characters described below (factorial multivariate analysis of variance (MANOVA), Pillai's trace, $p > 0.05$ for all), we pooled experimental replicates for each treatment. We then randomly selected 60 *P. amboinensis* recruits (10 individuals per night) from the light-trap catches in silent (control), high- and low-frequency sound treatments, respectively, and considered each fish as an individual. Fish size (standard length (SL), mm) and weight (g) were recorded following euthanasia prior to sagittal otolith extraction. Following extraction, each otolith pair was cleaned in distilled water, immersed in 70% alcohol and left and right otoliths stored dry in individual numbered wells for subsequent shape and FA analyses.

To obtain otolith shape characteristics, a calibrated grey-scale image of each sagittal otolith was captured, and the two-dimensional shape of left and right otoliths was

quantified using fast Fourier analysis. Briefly, this method calculates shape descriptors (also called 'harmonics', H_n) from the outline of the otolith images over 128 sampling points (Gagliano & McCormick 2004). By setting the zeroth descriptor (H_0) to zero, the first descriptor (H_1) to 1 and then dividing all successive harmonics by H_1 , we were able to standardize the first 15 harmonics to exclude any confounding effect of otolith image position and size from the data. The grey-scale images were also used to measure four other shape characters; maximum otolith length (μm), perimeter (μm), area (μm^2) and rectangularity, an index which calculates how well an otolith fits into a rectangular shape. For statistical analyses, we used all four shape characters and the first 15 standardized harmonics (H_2 – H_{16}), where H_2 – H_6 are referred to as low-order descriptors and determine the coarse outline shape of the otolith, whereas successively higher descriptors measure increasingly finer details of the otolith outline. The number of harmonics to be used as shape descriptors for the left and right otolith of each fish was set to the first 15 (excluding the zero and first harmonics) because the contribution of higher order harmonics (i.e. H_{17} and above) to the definition of the shape was negligible.

To determine whether the frequency of FA in the population changed during the larval phase, we used χ^2 -tests to compare the observed relative frequency of asymmetric and symmetric individuals of settlement-stage recruits (i.e. at the end of the larval phase) to the expected frequency of FA at hatching (i.e. at the beginning of the larval phase), assuming that the frequency of individuals with otolith pairs exhibiting symmetrical and asymmetrical shapes in the population at hatching does not change over time. To do so, we estimated a value of asymmetry for each of the 19 shape/size otolith descriptors for each individual in the control sample. Although the overall errors associated with obtaining measurements from the digital images were low (coefficient of variation (CV) values ranged between 0.3 and 7.8%), the extent of ME was conservatively removed by subtracting the mean ME specific to a descriptor from the mean FA value for that descriptor. As described previously, individuals yielding FA values greater than the ME specific to a trait were all classified as asymmetrical for that trait.

Using χ^2 -tests on all 19 otolith descriptors, we also determined whether observed frequencies of asymmetric and symmetric individuals of recruits caught in HF and LF sound traps, respectively, were significantly different from expected FA frequency, represented by fishes caught in the control treatment.

We then compared otolith FA of fishes caught in light traps broadcasting high-frequency sound with those caught in low-frequency sound traps using all 19 otolith descriptors in a multivariate analysis of variance (MANOVA). We used a stepwise discriminant function analysis to determine which otolith descriptors contributed the most to the discrimination between the two treatments and evaluated the statistical significance of those otolith descriptors using univariate analysis of variance (ANOVA) corrected for multiple comparisons ($\alpha = 0.05/k$, where k is the number of selected otolith descriptors).

To provide additional developmental information on individuals captured in high- and low-frequency traps, we examined the information stored within the otoliths of these individuals. Thin cross sections of otoliths were obtained by mounting individual otoliths in thermoplastic cement

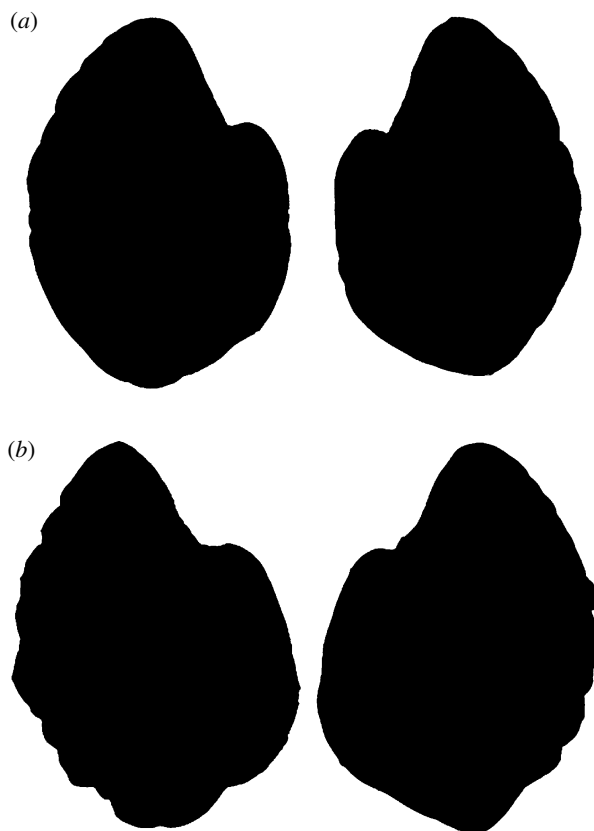


Figure 1. Bilateral asymmetry of shape in the otolith pairs of two representative *P. amboinensis*. (a) Fishes heading for high-frequency sounds had more symmetrical otolith pairs than (b) fishes attracted to low-frequency sounds.

(Crystal Bond) on a glass microscope slide and then grounding and polishing them using 12–0.3 μm lapping films. Sections were viewed using a compound microscope at 400 \times magnification and analysed by measuring the distance along the longest axis of the cross section by a video image analysis system linked to the microscope. In this species, a clear hatch mark is formed at the day of hatching and is the increment closest to the spherical nucleus of the otolith (Wellington & Victor 1989). The pelagic larval duration (PLD) is readily measured by counting the number of increments from the nucleus to the settlement mark (Bay *et al.* 2006) and the growth history of individual fish can be accurately described by measuring the distance between these increments (Wilson & McCormick 1997). Using a series of mixed model ANOVAs where collection night replicate was the random factor and the sound treatment (i.e. LF and HF) was the fixed factor, we tested for differences in otolith size-at-hatching (area, μm^2), PLD and pre-settlement individual growth history. Differences in fish body characteristics (SL and weight) were also tested (mixed model ANOVA).

3. RESULTS

At hatching, individuals with symmetrical (41%) and asymmetrical otoliths (59%) were equally represented among clutches (χ^2 -test, $p=0.203$). When we examined the otoliths of settlement-stage recruits collected in the control traps, 11 out of 19 otolith descriptors (i.e. H_2 , H_3 , H_5 , H_9 , H_{11} , H_{15} , H_{16} , maximum otolith length, perimeter, area and rectangularity) revealed that the

Table 1. One-way ANOVA results corrected for multiple comparisons on differences in otolith shape asymmetry between *P. amboinensis* recruits attracted to high- and low-frequency sound traps. Italic indicates significance at corrected $\alpha=0.008$.

variables	<i>F</i> -value	d.f.	<i>p</i>
<i>otolith descriptors</i>			
H_3	2.79	1,120	0.098
H_5	5.02	1,120	0.027
H_9	8.49	1,120	<i>0.004</i>
H_{11}	2.74	1,120	0.100
area	3.43	1,120	0.067
rectangularity	1.629	1,120	0.204

frequency of FA in the cohort returning to the reef at the end of the pelagic phase was significantly different from at hatching (χ^2 -tests, $p<0.05$ for all 11 traits). Indeed, we found that the cohort was consistently represented by a larger proportion of symmetrical recruits (63% on average across the 11 traits; up to 71% for H_{11}). Based on the remaining eight traits, we detected no change in frequency of FA between hatching and settlement (χ^2 -tests, all $p>0.05$). Although based on the significance of H_{11} alone, a comparison of the FA frequency between control and LF treatment indicated that traps broadcasting low-frequency sound attracted 18% fewer symmetrical recruits than control silent traps (χ^2 -test, $p<0.05$ for H_{11} ; all other traits showed no significant differences). On the other hand and even though based on the significance of only three descriptors, traps broadcasting high-frequency sound (HF) attracted between 9 and 18% more symmetrical recruits than silent traps (χ^2 -test, $p<0.05$ for $H_{7,12,13}$ only; all other traits showed no significant differences).

When we compared the two sound treatments, we recorded significant differences in the otolith shape asymmetry of fishes caught in traps broadcasting high- and low-frequency sound (HF and LF, respectively; Wilks' $\lambda=0.74$, $p<0.05$). Recruits attracted to traps broadcasting HF sound were more symmetrical than fishes caught in the LF sound trap (figure 1). Based on the discriminant function analysis, the two treatments could be clearly distinguished from each other on the basis of 6 out of 19 shape descriptors (H_3 , H_5 , H_9 , H_{11} , otolith area and rectangularity), which indicated that differences between individuals caught by HF and LF traps were mainly related to gross (low- to mid-order harmonics), rather than fine-scale (higher-order harmonics) differences in the asymmetry of otolith pairs. Specifically, harmonic H_9 revealed that recruits attracted by HF sound had significantly higher levels of symmetry compared with those caught in the LF treatment (table 1; figure 2). Although marginally non-significant (table 1), differences between HF and LF treatments in harmonics H_3 , H_5 and H_{11} as well as otolith area and rectangularity further suggested that individuals attracted by HF sound exhibited a consistently higher level of symmetry for these six traits (figure 2).

Interestingly, fishes attracted to LF traps also reached the reef after a longer pelagic larval phase than those caught in HF traps (mean PLD 18 and 16 days,

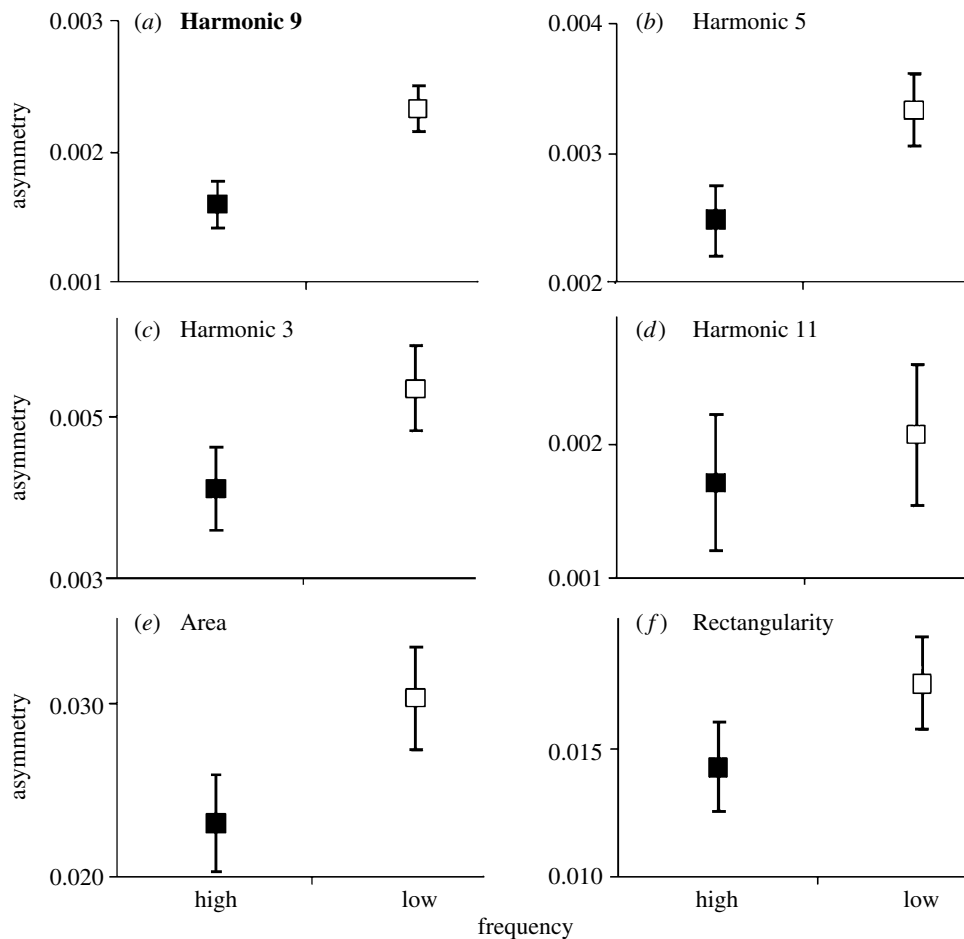


Figure 2. Comparison of the average degree of asymmetry in the otolith shape of *P. amboinensis* caught in traps broadcasting high (black filled squares) and low (open squares) frequency sound. Otolith traits for which significant differences ($p < 0.008$) in the level of asymmetry were detected are indicated in bold. Other traits also show that fishes attracted to low-frequency sound exhibit higher levels of otolith asymmetry. Error bars represent 95% CIs.

respectively; mixed model ANOVA, $F_{1,61} = 32.84$, $p < 0.002$). There were no significant differences in body size (mixed model ANOVA, $F_{1,155} = 1.13$, $p = 0.33$) or weight (mixed model ANOVA, $F_{1,155} = 3.48$, $p = 0.12$) of fishes caught in HF and LF traps. By examining the otolith growth history of individuals from the two treatments, we also found that fish attracted to either of the two traps did not grow differently or more rapidly throughout their pelagic phase (repeated-measure ANOVA, $F_{1,55} = 0.147$, $p = 0.70$). However, fish caught in LF traps had significantly larger otoliths prior to the pelagic phase (at hatching) than those from the HF traps (mean area was 450 and 380 μm^2 , respectively; mixed model ANOVA, $F_{1,62} = 13.04$, $p < 0.05$).

4. DISCUSSION

FA of morphological characters has often been proposed to be negatively associated with individual quality and fitness in a large range of taxa (e.g. Møller & Nielsen 1997; Martin & Lopez 2001; Bergstrom & Reimchen 2003). While most studies have examined the extent to which FA in characters that are important to intra- and inter-specific interactions may be a reliable indicator of individual quality and performance (e.g. Breuker & Brakefield 2002; Bergstrom & Reimchen 2003; Cornelissen & Stiling 2005), few studies have examined the potential functional costs of asymmetry and whether asymmetry influences dispersal and

recruitment processes (but see Matessi 1997; Breuker *et al.* 2007). Previous studies on asymmetry within fishes indicate that bilateral differences in otolith mass can trigger abnormal swimming behaviour ('motion sickness'; Helling *et al.* 2003) and interfere with correct sound localization (Lychakov & Rebane 2005), reducing an individual's ability to interact with its environment by compromising its performance. If variations in otolith size and shape do have a major bearing on an individual's ability to effectively detect sound (Popper & Lu 2000), what the present finding suggests is that asymmetrical otoliths may have a direct effect on the ability of *P. amboinensis* larvae to detect optimal reef habitats during the critical settlement phase of their lives. In the present study we propose that the occurrence of FA during the early life stages of reef fish interferes with the capacity, performance and efficiency of individuals recruiting to coral reefs.

We found that fishes caught in traps broadcasting LF sound were not only more asymmetrical, but they also reached the reef after a longer pelagic phase compared with conspecifics attracted to the HF sound. Firstly, one interpretation of the consequences of this result is that individuals with higher levels of asymmetry of the otolith pair could encounter more difficulties in detecting and orienting towards the reef habitat. And secondly, on reaching the reef there may be detours and delays in locating suitable settlement sites (Higgs 2005).

Undoubtedly, there are other alternative interpretations to explain our results, including differences in response threshold among individuals with different otolith size/shape, and in the locomotory ability of fishes to avoid predators once near the reef. Clearly, the relationship between otolith asymmetry and survival deserves further investigation. Regardless, each of these situations would undoubtedly result in an increased chance of mortality to the individual. These scenarios would support the hypothesis that the level of asymmetry is subject to selective pressure (e.g. Balmford *et al.* 1993; Swaddle 1997) and suggest that symmetrical individuals of this species have a strong survival advantage over asymmetrical individuals.

Our results indicated that asymmetry in the shape of *P. amboinensis* otoliths arose during their early development (i.e. 3–4 days of post-fertilization of the egg), supporting the recent findings by Lychakov *et al.* (2006) who have indicated that the level of otolith asymmetry in fishes is established at the very onset of growth of the paired otoliths (i.e. at the embryonic stage). Interestingly, these authors also suggested that asymmetry remains stable during a fish's lifetime (even in asymmetrical species, Lombarte 2007, personal communication). This is contrary to the expectation that asymmetry between the left and right sides can be corrected by developmental mechanisms of catch-up growth (i.e. compensatory growth hypothesis; Swaddle & Witter 1997, Kellner & Alford 2003). Based on the results of the present study, we found no evidence indicating that otolith asymmetry was corrected during the pelagic larval phase of this coral reef fish. Nonetheless, a recent study on the otolith shape of juvenile *P. amboinensis*, while not looking at asymmetry directly, suggested that otolith asymmetry could be manipulated by changing the feeding history of young fishes (Gagliano & McCormick 2004). Taking this into account, it seems probable that individuals are capable of modifying and possibly correcting their asymmetries and that such corrections may be possible during specific time windows in their life but not in others (i.e. the pelagic phase).

In our study, fishes attracted to LF and HF traps did not differ in body size, weight or otolith growth rates during their pelagic phase. However, they did differ in otolith size-at-hatching, where individuals from the LF treatment had larger otoliths at hatching than individuals from the HF treatment. The size of the otolith at hatching is indicative of differences in metabolic rates and individuals with larger otoliths at hatching have higher metabolic, and in turn, growth rates as embryos (Bang & Gronkjaer 2005; Bochdansky *et al.* 2005). If this is the case, then our results clearly demonstrate that rapid growth during this early phase can compromise the developmental programme of individual fish larvae and result in correspondingly higher levels of otolith asymmetry. Ultimately, the bilateral differences observed in *P. amboinensis* recruits established as early in life as the egg stage have significant carry-over effects, strongly influencing the survivorship potential of larvae and performance later in life as new reef recruits (cf. Gagliano *et al.* 2007).

While there has been considerable discussion over the consistency of the relationship between asymmetry and survival (reviewed by Swaddle 2003), the present findings show that asymmetry can be indicative of selective processes operating in the wild.

We recognize that an increase in the degree of asymmetry does not inevitably pose a serious cost to asymmetrical individuals. However, we agree with Downhower *et al.* (1990) in that if the more asymmetrical individuals are removed from a population before they can be sampled, the relatively low levels of asymmetry recorded in many animal populations may be the outcome of earlier selective processes (e.g. birds, Balmford *et al.* 1993; insects, Swaddle 1997; fishes, Lychakov *et al.* 2006). Because patterns of selection are directly related to individual phenotype, symmetrical individuals contribute relatively more to the next generation. Therefore, the occurrence of phenotypic selection favouring bilateral symmetry at crucial ontogenetic periods may well have important evolutionary repercussions on recruitment variability.

Although the importance of sound in recruitment processes has been established (Simpson *et al.* 2005a), the acoustic sensitivity and degree to which larvae can discriminate specific signature reef noises are still largely unknown. However, we do know that embryos respond to sound while developing in their benthic eggs (Simpson *et al.* 2005b), suggesting that the potential for imprinting and relating sound cues with their home reef sound signature exists. If so, we may soon be able to provide definitive evidence to link these new discoveries to self-recruitment processes. Here, our study has made a direct contribution to the question of how larval fishes find their way back to the reef by exploring one of the underlying mechanisms that ensure that larvae are well equipped to meet this challenge. We explored the nature and potential consequences of individual developmental trajectories on the navigational skills of larval reef fish and provided a physiological validation for the important role that asymmetry plays in dispersal and recruitment processes. Perhaps most importantly, we showed that asymmetries established during the embryonic life of reef fish are not amended by events in the subsequent pelagic growth history (cf. Gagliano *et al.* 2007). Ultimately, whether an individual is capable of compensational growth at a later stage or not becomes irrelevant if it does not survive past its larval stage. Investigating the relationship between asymmetry and recruitment processes may open an important door to understanding the natural dynamics of wild fish populations.

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